

Evolution of cooperation in multilevel public goods games with community structures

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Abstract. - In a community-structured population, public goods games (PGG) occur both within and between communities. Such type of PGG is referred as multilevel public goods games (MPGG). We propose a minimalist evolutionary model of the MPGG and analytically study the evolution of cooperation. We demonstrate that in the case of sufficiently large community size and community number, if the imitation strength within community is weak, i.e., an individual imitates another one in the same community almost randomly, cooperation as well as punishment are more abundant than defection in the long run; if the imitation strength between communities is strong, i.e., the more successful strategy in two individuals from distinct communities is always imitated, cooperation and punishment are also more abundant. However, when both of the two imitation intensities are strong, defection becomes the most abundant strategy in the population. Our model provides insight into the investigation of the large-scale cooperation in public social dilemma among contemporary communities.

Introduction. – How cooperation emerges and prevails in a selfish population poses a challenging problem in evolutionary biology as well as behavioral science [1, 2]. A powerful paradigm for investigating this problem in groups of interacting players of arbitrary size is public goods game (PGG) [3, 4]. In a PGG, each cooperator invests into a common pool while each defector attempts to exploit the public goods without any contributions. Thus, the payoff of a cooperator is always less than that of a defector. It is better off defecting than cooperating.

During the past few years, a number of mechanisms have been demonstrated analytically or experimentally to promote cooperation [3–11]. As an important mechanism, how spatial structure affects the evolution of cooperation has attracted much attention recently [12–14]. In structured populations, cooperators may form clusters to resist exploitation by defectors, resulting in the maintenance of cooperation. So far, most previous works of PGG in structured populations are based on lattice, small-world networks and scale-free networks. However, the study of

PGG in populations with community structure, which is a signature of the hierarchical nature of real social and biological systems [15, 16], has received little attention.

The so-called community structure consists of many groups, where interaction rate within group is higher than that between groups [15, 16]. Due to the community structure, it is straightforward to consider that games are not only played among community members, but also played among different communities. Each individual engages in not only the “local” PGG in its community, but also the “global” PGG played among distinct communities. Hence, individuals are simultaneously involved in multiple PGGs on different hierarchical levels [17–19]. These simultaneous local and global PGGs in a community-structured population constitute a multilevel PGG (MPGG).

Based on the MPGG, several straightforward questions arise: How to maintain cooperation in a large-scale among multiple communities? What is the effect of community structures on the evolution of cooperation? Some recent works have investigated the large-scale cooperation in PGG among contemporary societies by behavioral ex-

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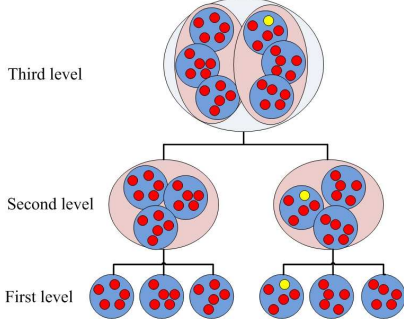


Fig. 1: (Color online) Sketch map of MPGG. On the first level, in each G_1 -community, five individuals play a PGG together; On the second level, in each G_2 -community, three G_1 -communities are involved in a larger PGG; On the third level, two G_2 -communities take part in the largest PGG.

periments [17–19] and simulation [20]. Some theoretical models are proposed to study the cooperation and punishment in infinite group-structured populations by deterministic analysis [21]. However, finite population size is proved to bring internal noise which drives the population dynamics off the deterministic trajectory in the infinite situations [22, 23]. Thus, a mathematical model of how community structures affect the evolution of cooperation in finite populations is still lacking.

Motivated by these, we propose a minimalist evolutionary model of MPGG and analytically study the evolution of cooperation in finite populations with such community structures where the interaction within community is far more frequent than that between communities. We adopt imitation updating rule and explore how the imitation strength within community and that between communities influence the evolutionary of cooperation. We demonstrate that under the condition of sufficiently large community size and community number, if the imitation strength within community is weak, or that between communities is strong, cooperation can prevail in the population. Nevertheless, if both of the imitation strengths are strong, defection is the unique favorable strategy. Furthermore, when the imitation within community is moderate, small imitation between communities may favor punishers prevailing while cooperators nearly disappear.

Model. — Consider a finite population with community structures in which individuals take part in an n -level PGG. In this population, every m_1 individuals form a community, and any two such communities have no common member. Denote this type of communities by G_1 . Moreover, every m_2 G_1 -communities constitute a larger community denoted by G_2 . This similar formation process repeats until m_n G_{n-1} -communities make up a G_n -community which is the entire population. According to the above formation rule, this population is characterized by a hierarchical structure (see fig. 1).

We first study the simplest case with only two strategies: cooperation and defection (the case with punishment

will be added and described later). A MPGG is played as follows: on the first level, in each G_1 -community, m_1 individuals play a PGG together. Each cooperator contributes c into the public pool in the G_1 -community to which this player belongs, and every defector donates nothing. The total amount in this public pool is separated into two parts: one portion, whose proportion is k_1 , is allocated to the local PGG in this G_1 -community, and the other portion, whose proportion is $1 - k_1$, is contributed into a higher public pool in the larger G_2 -community which contains this G_1 -community. The total contribution in this local PGG is multiplied by an enhancement factor r_1 , and the product is distributed equally among all players in this G_1 -community no matter whether they contribute or not.

On the second level, in each G_2 -community, m_2 G_1 -communities engage in a larger PGG. Each G_1 -community contributes a fraction of the total amount (the proportion is $1 - k_1$), which is collected in the PGG among its members, into the public pool in G_2 -community which contains this G_1 -community. Then, the total amount in this public pool in G_2 -community is also divided into two parts: one part whose proportion is k_2 is contributed to the PGG in this G_2 -community and the other part is submitted to the higher public pool in the G_3 -community on the third level. The first part is multiplied by an enhancement factor r_2 , and the product is distributed among all individuals in this G_2 -community.

Such type of PGG repeats until the highest level. On the highest level, the total amount in the public pool in G_n -community is contributed into the global PGG. This amount is multiplied by an enhancement factor r_n , then the product is distributed among the entire population. Although cooperators only contribute in the G_1 -community on the lowest level, their contributions are allocated in n different PGGs at hierarchical levels. The payoff of each individual, irrespective of cooperators and defectors, is derived from n PGGs.

Individuals in the population adjust their strategies through imitation. At each time step, two players i and j are randomly chosen. These two players belong to the same G_1 -community with the interaction rate q_1 . The probability that individual i adopts the strategy of j is given by $1/\{1 + \exp[-w_1(F_j - F_i)]\}$, where $w_1 \geq 0$ denotes the imitation strength between two players in the same G_1 -community, F_i and F_j are the payoff of individual i and j [7]. The imitation strength measures the dependence of decision making on the payoff comparison. For $w_1 \rightarrow 0$, individual i imitates the strategy of j almost randomly, which is referred as “weak imitation”. For $w_1 \rightarrow \infty$, a more successful player is always imitated, which is referred as “strong imitation”.

Moreover, if the two players do not belong to the same G_1 -community, but they are part of the same G_2 -community, the interaction rate for these two players is q_2 . In this case, player i imitates the strategy of j with the probability $1/\{1 + \exp[-w_2(F_j - F_i)]\}$, where w_2 is the imitation strength between two players from different G_1 -

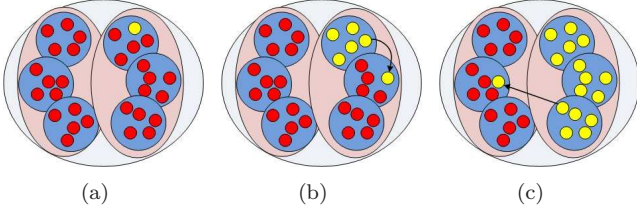


Fig. 2: (Color online) Fixation process of a single mutant in a population. (a) A single mutant is produced in the population; (b) This mutant successfully takes over its G_1 -community, and another individual from other G_1 -communities imitates the mutant's strategy; (c) The mutant successfully invades its G_2 -community, and another one from other G_2 -communities imitates the strategy of the mutant. This type of fixation and imitation repeat until the population full of one type of players.

communities but in the same G_2 -community. In general, the interaction rate for two players belonging to different G_l -communities ($l = 1, \dots, n-1$) but in the same G_{l+1} -community is q_{l+1} . The relationship $\sum_{l=1}^n q_l = 1$ needs to be satisfied. In this case, player i changes its strategy to j 's with the probability $1/\{1 + \exp[-w_{l+1}(F_j - F_i)]\}$ ($l = 1, \dots, n-1$), where w_{l+1} denotes the imitation strength between two G_l -communities. Since we focus on such community structure where the interaction within community is far more frequent than that between communities, we assume $q_1 \gg q_2 \gg \dots \gg q_n$.

For finite populations, we analyze the advantage of a strategy through fixation probability, which measures the probability for a single mutant using such focal strategy to successfully take over the resident population. In order to obtain a general expression, we suppose there are two types of strategies, A and B . Imagine that a mutant adopting strategy A is produced in a population of B players. Since $q_1 \gg q_2$, the time that this mutant takes over the G_1 -community to which it belongs or disappears is shorter than that two individuals from different G_1 communities meet. The time scales of fixation in a G_1 -community and imitation between two individuals from different G_1 -communities are separated. Thus, fixation of this mutant A in the population goes through several stages described by fig. 2.

Actually, the fixation process of a single A mutant in a population is equivalent to only n steps: the fixation of this A mutant in its G_1 -community; The fixation of this G_1 -community composed entirely of A players in its G_2 -community;...; The fixation of the G_{n-1} -community invaded by the A mutant in the whole population.

Denote the fixation probability of a single A mutant invading a G_1 -community of B players by ρ_{BA}^1 . This fixation probability ρ_{BA}^1 equals

$$\rho_{BA}^1 = \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp\{w_1 \sum_{i=1}^j [F_B^1(m_1-i) - F_A^1(i)]\}}, \quad (1)$$

where $F_A^1(i)$ and $F_B^1(m_1-i)$ are the payoff of each A player and each B player in the focal G_1 -community, respectively,

when there are i A players and $m_1 - i$ B players in this G_1 -community [24].

Denote the fixation probability of a G_1 -community full of A players in its G_2 -community of only B individuals by ρ_{BA}^2 . Suppose there are i G_1 -communities consisting of only A players and $m_2 - i$ G_1 -communities of only B players. In this focal G_2 -community, the payoff of each A player is denoted by $F_A^2(i)$ and that of each B player is $F_B^2(m_2 - i)$. A new G_1 -community full of A players arises when two players with different strategies from different G_1 -communities are chosen, and the B player alters its strategy through imitation, then it takes over its G_1 -community. Thus, the probability to increase the number of G_1 -communities full of A players by one is given by

$$\Gamma_A^+(i) = q_2 \frac{i}{m_2} \frac{m_2 - i}{m_2} \frac{\rho_{BA}^1}{1 + \exp\{-w_2[F_A^2(i) - F_B^2(m_2 - i)]\}}.$$

Similarly, the probability to decrease the number of G_1 -communities full of A players by one is

$$\Gamma_A^-(i) = q_2 \frac{i}{m_2} \frac{m_2 - i}{m_2} \frac{\rho_{AB}^1}{1 + \exp\{-w_2[F_B^2(m_2 - i) - F_A^2(i)]\}}.$$

The fixation probability of a G_1 -community full of A players in a G_2 -community is obtained as follows

$$\rho_{BA}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp\{w_2 \sum_{i=1}^j [F_B^2(m_2-i) - F_A^2(i)]\} (\rho_{AB}^1 / \rho_{BA}^1)^j}.$$

In general, denote the fixation probability of a single A mutant in a G_l -community consisting of only B players ($l = 2, \dots, n$) by Φ_{BA}^l . Accordingly, we have

$$\Phi_{BA}^l = \rho_{BA}^1 \times \rho_{BA}^2 \times \dots \times \rho_{BA}^l, \quad (2)$$

where

$$\rho_{BA}^l = \frac{1}{1 + \sum_{j=1}^{m_l-1} \exp\{w_l \sum_{i=1}^j [F_B^l(m_l-i) - F_A^l(i)]\} (\rho_{AB}^{l-1} / \rho_{BA}^{l-1})^j}.$$

Two-level PGG with punishment. — We now consider two-level PGG. Suppose three available strategies in this PGG: cooperation, defection and punishment. Punishers are such type of players which contribute as cooperators but reduce the payoff of defectors with a cost to themselves. We focus on the situation without second-order punishment which does not punish cooperators [7].

In each G_1 -community, punishment acts as a personal behavior. Its object is defectors. Each punisher imposes a fine β_1 on each defector at a cost γ_1 ($\gamma_1 < \beta_1$) to itself. The total fine for a defector relies on the number of punishers in this G_1 -community, whereas the total cost for a punisher is determined by the number of defectors.

Furthermore, for the separation of time scales, communities always stay in homogeneous states. If a homogeneous community is composed of punishers, they act as an institute of punishment. This institute of punishment punishes those communities consisting of defectors even

also containing cooperators or punishers since such communities free-ride on the global public goods. Specifically, a community full of punishers punishes those communities where defectors exist. Each punishing community reduces the total payoff of each punished community by $m_1\beta_2$, at a total cost $m_1\gamma_2$ ($\gamma_2 < \beta_2$). Then, the cost of punishing is shared by all punishers in this punishing community, whereas the fine on the punished community is distributed among its members. Hence, the total fine for each individual in the punished communities depends on the number of the punishing communities, while the total cost for each punisher in the punishing communities is determined by the number of the punished communities.

Although the strategy updating is mainly dependent on imitation, mutation of strategies may happen sometimes. At each time step, every individual may mistakenly switch its strategy to a different and random strategy with the probability μ . Suppose the mutation rate $\mu \rightarrow 0$. Sufficiently small μ assures that a single mutant vanishes or fixes in a population before the next mutant appears. The population is homogeneous most of the time [5, 24, 25]. Therefore, in the limit of rare mutations, the evolutionary process of consideration can be approximated by a Markov chain where the state space is composed of homogeneous states full of each type of players. In this case, the state space of this Markov chain contains homogeneous state of cooperators, that of defectors and that of punishers. The corresponding transition probability matrix is

$$\Lambda = \begin{pmatrix} 1-\Phi_{CD}^n-\Phi_{CP}^n & \Phi_{CD}^n & \Phi_{CP}^n \\ \Phi_{DC}^n & 1-\Phi_{DC}^n-\Phi_{DP}^n & \Phi_{DP}^n \\ \Phi_{PC}^n & \Phi_{PD}^n & 1-\Phi_{PC}^n-\Phi_{PD}^n \end{pmatrix}. \quad (3)$$

The normalized left eigenvector corresponding to the eigenvalue 1 of the matrix Λ determines the stationary distribution, which describes in the long run, the percentage of time spent by the population in each homogeneous state. The stationary distribution for the above transition matrix eq. (3) can be calculated as follows

$$\begin{aligned} X_C &= \frac{\Phi_{PC}^n\Phi_{DP}^n + \Phi_{PC}^n\Phi_{DC}^n + \Phi_{DC}^n\Phi_{PD}^n}{\Delta} \\ X_D &= \frac{\Phi_{PC}^n\Phi_{CD}^n + \Phi_{CD}^n\Phi_{PD}^n + \Phi_{CP}^n\Phi_{PD}^n}{\Delta} \\ X_P &= \frac{\Phi_{CP}^n\Phi_{DC}^n + \Phi_{CD}^n\Phi_{DP}^n + \Phi_{CP}^n\Phi_{DP}^n}{\Delta}, \end{aligned} \quad (4)$$

where X_C , X_D , and X_P denote the probability to find the population in the homogeneous state consisting entirely of cooperators, defectors, and punishers, respectively, the normalization factor Δ insures $X_C + X_D + X_P = 1$.

We only discuss the situation of a two-level PGG in detail. In the case of no defectors, since punishers do as the same as cooperators under the condition of no second-order punishment, these two types of players are of no difference. This situation can be viewed as “neutral case”, where the fixation probability of a neutral mutant equals the reciprocal of the population size [26], that is, $\Phi_{CP}^2 = 1/(m_1m_2)$ and $\Phi_{PC}^2 = 1/(m_1m_2)$.

The fixation probabilities Φ_{DC}^2 , Φ_{CD}^2 , Φ_{DP}^2 and Φ_{PD}^2 are given as follows:

$$\Phi_{DP}^2 = \rho_{DP}^1 \times \rho_{DP}^2$$

$$\frac{1}{\rho_{DP}^2} = 1 + \sum_{j=1}^{m_2-1} \exp\{w_2 \sum_{i=1}^j [c + \gamma_2 m_2 - ck_1 r_1 - (\beta_2 + \gamma_2)i]\} \times \left(\frac{\rho_{PD}^1}{\rho_{DP}^1}\right)^j,$$

$$\Phi_{DC}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp(\Theta j)} \times \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp(w_1 c j)},$$

$$\Phi_{CD}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp(-\Theta j)} \times \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp(-w_1 c j)},$$

$$\Phi_{PD}^2 = \rho_{PD}^1 \times \rho_{PD}^2$$

$$\rho_{PD}^1 = \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp\{w_1 \sum_{i=1}^j [(m_1 - i)\beta_1 - c - i\gamma_1]\}}$$

$$\frac{1}{\rho_{PD}^2} = 1 + \sum_{j=1}^{m_2-1} \exp\{w_2 \sum_{i=1}^j [ck_1 r_1 + \beta_2 m_2 - c - (\beta_2 + \gamma_2)i]\} \times \left(\frac{\rho_{DP}^1}{\rho_{PD}^1}\right)^j.$$

where $\Theta = c[w_2(1 - k_1 r_1) + w_1(m_1 - 1)]$.

Note that when $w_1 \rightarrow 0$ and w_2 is not weak, the relationship $\Phi_{CD}^2 < \frac{1}{m_1 m_2} < \Phi_{DC}^2$ is always satisfied in the case of $k_1 r_1 > 1$. Besides, when $w_2 \rightarrow \infty$ and w_1 is limited, there is $\Phi_{DC}^2 > \Phi_{CD}^2$ in the case of $k_1 r_1 > 1$. It indicates that in these two situations, cooperation is more abundant than defection [27]. Except for these two conditions, defection is always more abundant than cooperation. In addition, when $m_1 \gamma_1 \gg c$ and $m_1 \beta_1 \gg c$, the inequality $\Phi_{DP}^1 > \Phi_{PD}^1$ is always satisfied. Furthermore, when $m_2 \gamma_2 \gg c - ck_1 r_1$ and $m_2 \beta_2 \gg ck_1 r_1 - c$, the relationship $\rho_{DP}^2 > \rho_{PD}^2$ always holds, regardless of the imitation strengths w_1 and w_2 . Hence, if m_1 and m_2 are sufficiently large, punishers are always more abundant than defectors.

Based on the stationary distribution, we find that when m_1 and m_2 are sufficiently large, weak imitation within G_1 -community or strong imitation between G_1 -communities is of great benefit to cooperators and punishers (see fig. 3). In these two cases, cooperators do as well as punishers, they are both more abundant than defectors. However, if these two imitation strengths are both strong, it is harmful to the evolution of cooperation and punishment. Moreover, in the case of moderate imitation strength w_1 , small w_2 may favor punishers prevailing but has a little effect on the emergence of cooperation (see fig. 4(a)). Furthermore, when w_2 is moderate, the preservation of cooperators and punishers are hindered. When w_2 is large enough, cooperation and punishment are still more abundant than defection.

The reason for the above phenomenon is that under the condition $k_1 r_1 > 1$, weak w_1 incurs $\Phi_{DC}^2 > \Phi_{CD}^2$, and the inequality $\Phi_{DP}^2 > \Phi_{PD}^2$ always holds for sufficiently large m_1 and m_2 . Based on eq. (4), we obtain $X_C > X_D$ and $X_P > X_D$ for weak w_1 . In this case, the population spends

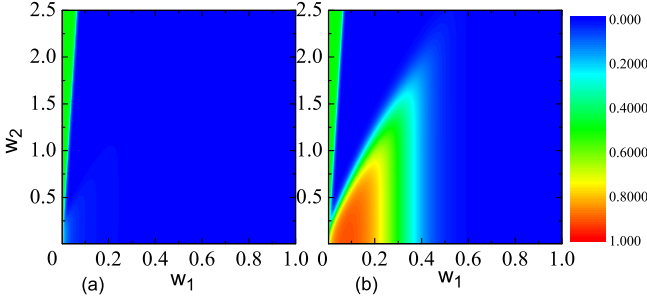


Fig. 3: (Color online) Stationary distribution as functions of imitation strengths w_1 and w_2 . (a) Probability X_C ; (b) Probability X_P . Probability X_D can be derived from $X_C + X_D + X_P = 1$. Weak w_1 or strong w_2 is favorable for the prevalence of cooperators as well as punishers. However, if both imitation strengths are strong, it is harmful to the emergence of cooperation and punishment. Parameters: $c = 0.8$, $k_1 = 0.5$, $r_1 = 3$, $\beta_1 = 1$, $\gamma_1 = 0.5$, $\beta_2 = 1$, $\gamma_2 = 0.5$, $m_1 = 20$, and $m_2 = 20$.

most time in homogeneous state of cooperators or punishers. We state that our below results are all based on the assumption of sufficiently large m_1 and m_2 . Note that $k_1 r_1$ denotes effective enhancement factor within community. Only when the effective enhancement factor larger than one, cooperation may be favored in the long run. This condition $k_1 r_1 > 1$ is consistent with that in [3]. Moreover, when w_1 is moderate ($w_1 = 0.1$ in fig. 4(a)), small w_2 leads to the inequality $\Phi_{DC}^2 < \Phi_{CD}^2$. However, there is always $\Phi_{DP}^2 > \Phi_{PD}^2$. It indicates that defectors are more abundant than cooperators while punishers are superior to defectors. Note that punishment and cooperation are equal. Which one is the most favorable strategy depends on the comparison between Φ_{CD}^2 and Φ_{DP}^2 . Denote the ratio Φ_{CD}^2/Φ_{DP}^2 by K . From fig. 4(b), the rising K leads to decreasing X_P as well as X_C , but increasing X_D . When the gap between Φ_{CD}^2 and Φ_{DP}^2 is sufficiently small, the population spends its most time staying in the homogeneous state of punishers. With the increase in this gap, the advantage of defection over cooperation is enhanced, or that of punishment over defection is weakened. Consequently, defectors become more and more frequent than punishers and cooperators. However, when the imitation strength w_2 reaches so large that makes the inequality $\Phi_{DC}^2 > \Phi_{CD}^2$ satisfied, defectors perform the worst, the population is most likely to be found in the homogenous state full of cooperators or punishers with nearly equal probabilities.

Large imitation strength w_2 can also be viewed as positive out-group attitude which shows preference for individuals from other communities, while weak w_2 can be seen as neutral out-group attitude. From fig. 4(a), neutral out-group attitude is of great benefit to punishment but harmful to the evolution of cooperation. The impact of positive out-group attitude on the evolution of punishment is complicated. With an enhanced positive out-group attitude,

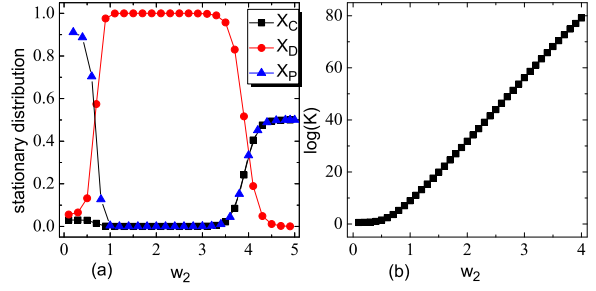


Fig. 4: (Color online) (a) Stationary distribution as a function of imitation strength w_2 in the case of moderate $w_1 (= 0.1)$. Strong w_2 makes cooperators and punishers more abundant than defectors. Besides, small w_2 also promotes punishment to be the most abundant strategy. However, moderate w_2 is harmful to both cooperators and punishers. (b) The ratio between Φ_{CD}^2 and Φ_{DP}^2 as a function of imitation strength w_2 when $w_1 = 0.1$ in the case of $\Phi_{DC}^2 < \Phi_{CD}^2$. The ratio K sustainably rises. It leads to the decrease of X_P as well as X_C and the increase of X_D when $\Phi_{DC}^2 < \Phi_{CD}^2$. Parameters in these two figures are the same as those in fig. 3.

punishment is favored at first, then its amount shrinks and rises finally. When the preference of individuals for those in other communities is sufficiently large, cooperation is also greatly favored.

Discussions and Conclusions. — we have proposed a minimalist theoretical model of MPGG in finite populations with community structures and explored under what circumstances the assortment of cooperation can be achieved in community-structured populations. We found that if the community size and the community number are both sufficiently large, weak imitation within community or strong imitation between communities promotes the prevalence of cooperation. This can be attributed to the principle that weak imitation within community may lead to assortment of cooperators, while strong imitation between communities assures the prevalence of cooperative behavior once a cluster of cooperators appears. However, if the imitation strengths within and between communities both become strong, cooperation as well as punishment are eliminated from the population. In addition, it is interesting that when the imitation within community is moderate, small imitation between communities makes punishers extraordinarily abundant in the population but cooperators nearly disappear.

A model relevant to ours is from ref. [28], where Traulsen and Nowak studied the effect of multilevel selection on the evolution of cooperation in Prisoner's Dilemma (PD), a classic two-person game. Compared with this model, we focus on PGG, a multi-person game, which has different ingredients and background from PD. Moreover, in [28], the game only occurs in each group, and there is no interaction between any two individuals from different groups. However, in our model, game exists not only in each com-

munity but among different communities. Besides, interactions always happen between individuals from distinct communities. It incurs the prevalence of a strategy across community. For the strategy updating rule, Moran process is applied in [28] while we adopted imitation process. Although the approximate expressions of fixation probability in these two different processes in the limit of weak selection are almost identical [29], those in the case of a moderate selection are extraordinarily different from each other. In addition, according to the evolution process, we obtain the essential difference between the model in [28] and ours as the mechanism to promote cooperation: the former is group selection whereas the latter is spatial selection. Group selection is suitable for the situation where individuals compete within groups and groups also compete with each other; Spatial selection is valid when there is only assortment of cooperators and no group level of selection [30]. In our model, there is no competition among communities and no selection at group level. Thus, this is not group selection but spatial selection.

Another similar concept to the community-structured population in biology is metapopulation [31]. Although both metapopulation and the community-structured population can be viewed as group-structured population, the mechanisms for the evolution of populations in these two types of models are different. The evolution of species in metapopulation is driven by recolonization and extinction, i.e., birth and death process in biology, while the evolution of cooperation in our work is inspired by imitation which is a behavior in sociology. In addition, we consider a simple type of punishment in this paper, which solely punishes defectors. In this case, cooperators become second-order free-riders since they exploit the sacrifice of punishers. Thus, cooperation should also be punished. Sigmund *et al.* shew that incorporating second-order punishment, which punishes both defectors and cooperators, the evolutionary dynamics can be drastically altered [7]. Besides, amount of empirical evidences reveal that defectors sometimes punish cooperators [32]. The corresponding population dynamics can be qualitatively changed by this “anti-social punishment” [33]. Therefore, to explore the effects of second-order punishment and antisocial punishment on the evolution of cooperation deserves more attention in future studies.

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